THE ACULEATE WASPS AND BEES OF CROW WOOD, FINNINGLEY IN WATSONIAN YORKSHIRE, WITH THE INTRODUCTION OF A NEW NATIONAL OUALITY SCORING SYSTEM

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Crow Wood has been found to be an excellent locality for aculeate wasps and bees, having 135 recorded species, nine species of national importance, and 15 species of regional significance.

Crow Wood, an area of about 152 ha, is situated immediately to the south of Finningley (VC63, SK6697). The region has sandy acid soils of remnant heathland. At present, Crow Wood consists of old sand and gravel pits gradually being filled with waste materials, coniferous afforestation, regenerating woodland with flowery areas, open sandy surfaces, some of which are used as motor-cycle and go-kart tracks, grassland, and arable farming. The dry open areas with ditches and mounds of sand and gravel provide nesting areas for many aculeate wasps and bees.

About 50 visits have been made to Crow Wood, mainly during May, June, July, and August, with a few during March, April, and September. Most visits were made by J.T. Burn (1971–1991: in excess of 36 visits to a sample area of about 18 ha) and M.E. Archer (1986–1989: 10 visits to a sample area of about 55 ha). Collecting was by visual observation, but J.T. Burn also collected by sweeping low mixed vegetation. A smaller number of visits were made by J.H. Flint (1965) and P. Skidmore (1973).

Biological names are according to Kloet & Hincks (1978), except for the Dryinidae which are according to Olmi (1984, 1989).

This paper was written by M. E. Archer (M.E.A.). The contributions of J.T. Burn were the many records from his large number of visits, and all information relating to the Bethylidae and Dryinidae.

RESULTS—SPECIES PRESENT AT CROW WOOD

A full list of recorded species is given in the Appendix. The taxonomic distribution is given in Table 1, at the family level. The 135 species represent about 46% of the aculeate wasp and bee species (including the bethylids and dryinids) of Watsonian Yorkshire. In addition the following ant species (Formicidae) have been recorded: Myrmica ruginodis Nylander, Formica fusca L., Lasius niger (L.).

The accumulated records from any locality can be analysed to understand the ecological relationships of the recorded species and the conservation value of the locality in a regional or national context. This paper assesses ecological relationships with the concepts of cleptoparasitic load and aerial nester frequency and conservation value with the aid of regional and national quality scores and species quality scores.

QUALITY ASSESSMENT OF SOLITARY SPECIES

Two species are nationally rare or 'red data book species' (Falk, 1991). Both of these, *Psen bicolor* (RDB2) and *Nomada fulvicornis* (RDB3), reach the northern boundary of their British distribution in Watsonian Yorkshire.

Table 1. The number of species of aculeate wasps and bees recorded from Crow Wood.

Family	No. species
Solitary wasps	
Dryinidae	14
Bethylidae	2 7
Chrysididae	7
Mutillidae	1
Pompilidae	12
Eumenidae	4
Sphecidae	36
Total solitary wasps	76
Solitary bees	
Colletidae	3
Andrenidae	17
Halictidae	13
Megachilidae	2
Anthophoridae	10
Total solitary bees	45
Total solitary wasps & bees	121
Social wasps and bees	
Vespidae	5
Apidae	9
Total social wasps & bees	14

Seven species are nationally scarce or notable species (Falk, 1991). Andrena tibialis, which is a category A scarce species, reaches the northern boundary of its British distribution in Watsonian Yorkshire. The other six species, which are category B species, are either at the northern boundary of their distribution (Cleptes semiauratus, Priocnemis schioedtei, Nysson trimaculatus, Andrena humilis, Nomada flavopicta), or are more widespread in Britain (Crossocerus palmipes).

Fifteen species are rare in the context of Watsonian Yorkshire (Archer, 1993a);

these are indicated in the Appendix.

There are 27 species of solitary wasps and bees, which although not rare in Watsonian Yorkshire, have a local distribution being more or less restricted to sandy habitats (Archer, 1994a). Seventeen of these local species (indicated in the Appendix) are found at Crow Wood.

The 105 species of solitary wasps and bees can be considered to have a common, frequent, occasional or rare status in Watsonian Yorkshire (Archer, 1993a) (Table 2). The dryinid and bethylid species cannot be given a status as insufficient information

Table 2. The regional coding of the 105 species of solitary wasps and bees recorded from Crow Wood (Dryinids and Bethylids excluded).

Status	No. spe	ecies
Common	39	
Frequent	31	
Occasional	20	
Rare	15	

exists on their distributions. By giving each species a value depending on the above statuses, including a higher value for the nationally scarce and rare species, a regional quality score of 416 can be calculated by the addition of the status scores (Table 3). Dividing this quality score by the 105 species gives a regional species quality score of 4.

Table 3. The regional status scheme of the 105 species of solitary wasps and bees recorded at Crow Wood.

Status	Status value (A)	No. species (B)	Status score (A×B)
Common	1	38	38
Frequent	2	31	62
Occasional	4	19	76
Rare	8	8	64
Nationally scarce	16	7	112
Nationally rare	32	2	64
		105	416

Summation of status value times number of species gives a final regional quality score of 416. Dividing this by the number of species (105) gives a regional species quality score of 3.96, approximately 4.

Ball (1992) proposed a methodology for scoring the value of invertebrates at sites in a national context. Archer (in press) has adopted this methodology for use in Watsonian Yorkshire. Using the Ball methodology on the 105 Crow Wood species, a national quality score of 274 and a national species quality score (274 \pm 105) of 2.6 can be calculated (Table 4).

Table 4. The Ball (1992) national status evaluation of the 105 species of solitary wasps and bees recorded at Crow Wood.

Status	Status value (A)	No. species (B)	Status score (A×B)
Common	1	62	62
Local	2	26	52
Regional notable	4	8	32
Scarce B	8	6	48
Scarce A	16	1	16
Rare	32	2	64
		105	274

Two objections can be raised against the Ball methodology. First, many regions of England and Wales lack a list of regionally notable species making it sometimes impossible to apply Ball's methodology. Secondly, a national scheme should logically give a species status based upon that species' importance in a national and larger geographical setting but not in a smaller or regional distribution.

To overcome the above two objections M.E.A. suggests the following scheme in which the statuses of 'common', 'local' and 'regionally notable' of Ball are replaced by: 'universal', 'widespread' and 'restricted'. At present there is no objective way of assigning a 'universal', 'widespread' or 'restricted' status to the species of the British aculeate Hymenoptera. From personal experience M.E.A. has therefore assigned

British aculeate Hymenoptera one of these three statuses based upon abundance and distribution within England and Wales, Ireland, the Channel Islands and Scotland have not been included: little information is available on Irish distributions of aculeate Hymenoptera; fauna of the Channel Islands relates more to France than the British Isles: and Scotland's cooler climate greatly reduces diversity. A 'universal species' would therefore refer to a common species found throughout England and Wales, usually with some extension into Scotland. A 'widespread species' would be one found in about three-quarters of England and Wales, usually either with a distribution in Wales, southern and midland England or in northern and western England and Wales. A 'widespread species' would also be found throughout England and Wales but either with a local distribution or a less-than-common abundance, A 'restricted species' would be one mainly found in about one-half of England and Wales, and usually confined to southern England and East Anglia. The status of a species may not be fixed and can change as its range or abundance changes. As such the statuses of species need to be kept under constant review. Using this new methodology for the 105 Crow Wood species a national quality score of 266 and a national species quality score (266 ÷ 105) of 2.5 can be calculated (Table 5).

Table 5. The Archer national status scheme of the 105 species of solitary wasps and bees recorded at Crow Wood.

Status	Status value (A)	No. species (B)	Status score (A×B)
Universal	1	56	56
Widespread	2	39	78
Restricted	4	1	4
Scarce B	8	6	48
Scarce A	16	1	16
Rare	32	2	64
		105	266

CLEPTOPARASITIC LOAD

The cleptoparasitic load (CL) is the percentage of aculeate species that are cleptoparasites (or parasitoids) on other host aculeates (Table 6). A more-or-less complete list of species in a locality should be made before the CL is calculated to avoid possible bias of either host or cleptoparasitic species. *Cleptes semiauratus*, dryinids and bethylids are not considered as they are parasitoids on non-aculeate hosts. *C. semiauratus* is a parasitoid on the cocoons of sawflies, e.g. *Nematus ribesii* (Scop.). The two bethylid species are parasitoids on lepidopterous larvae. *B. cephalotes* has been recorded using hollowed-out plant stems to shelter its larvae while feeding on its paralysed host. Dryinids are predators and parasitoids of Homoptera Auchenorrhyncha.

Table 6. The relative frequency of the eleptoparasitic species among the solitary wasps and bees from Crow Wood.

	No. hosts (H)	No. cleptoparasites (C)	Cleptoparasitic load $CL = 100 \times C/(H+C)$
Solitary wasps	49	10	16.9
Solitary bees	32	13	28.9

The CL for the species of solitary bees is higher than the CL for the species of solitary wasps.

AERIAL NESTER FREQUENCY

The aerial nester frequency (AF) is the percentage of host aculeate species that have aerial nest sites. Again a more-or-less complete list of species in a locality should be made before the AF is calculated to avoid possible bias of either aerial or subterranean nesters. Aerial nests are often in old beetle burrows in dead wood, or the central cavities of stems such as those of bramble. Subterranean nesters nest in the soil, usually in burrows dug by themselves, but sometimes in crevices or pre-formed burrows. The AF for the species of solitary wasps is higher than the AF for the species of solitary bees (Table 7).

Table 7. The nesting habits of the host solitary wasp and bee species from Crow Wood.

	No. aerial nesters (A)	No. subterranean nesters (S)	Aerial nester frequency $AF = 100 \times A/(A + S)$
Solitary wasps	10	39	20.4
Solitary bees	3	29	9.4

DISCUSSION. QUALITY ASSESSMENT

The regional and national status schemes of Ball and Archer respectively can be applied to other sandy habitats in Watsonian Yorkshire (Archer, 1984, 1985, 1988, 1989, 1992b, in press), Lincolnshire (Risby Warren, Archer, 1994b), Nottinghamshire (Sherwood Forest, Archer, in press) and Leicestershire (Charnwood Forest, Archer, 1992a). These sites are compared in Table 8. These sandy habitats vary greatly in size from the sand pit at Swincarr Plantation to the eroded Precambrian mountain range of Charnwood Forest. The number of species of aculeate wasps and bees varies from 35 species at Swincarr Plantation to 147 species at Charnwood Forest. The records are from recent times except for the records from pre-coniferized Allerthorpe Common which date from the 1920s until the 1950s and Charnwood Forest which date from the beginning of the twentieth century until the present. Since species status depends upon the current distribution and abundance of species, species only recorded in earlier times could be assigned the wrong status if the distribution or abundance of a species has changed.

The national quality and species quality scores derived from the Ball and Archer status schemes respectively, for each locality, are of a very similar or even of the same value (Table 8). Crow Wood on its species quality score is ranked fourth on the Ball scheme and equal fourth with Strensall Common on the Archer scheme, out of the eleven data sets. Both schemes would seem suitable as a national status scheme, but the Archer scheme is preferred for the reasons given earlier.

In the context of Watsonian Yorkshire, and considering the number of species, regional quality score, regional species quality score, and the number of national scarce and rare species (Table 8), Crow Wood is ranked second in importance behind preconiferized Allerthorpe Common. Since pre-coniferized Allerthorpe Common is no longer in existence, Crow Wood must now be considered the most important sandy locality for aculeate Hymenoptera in Watsonian Yorkshire.

Table 8. A comparison of the criteria of diversity, rarity and area of sandy habitats in Watsonian Yorkshire and elsewhere in England based on the species of solitary wasps and bees (dryinids and bethylids excluded).

Swincarr Plantation	0.05	-	74 2.1	57	62 1.8
Skipwith	312	2	149	105	109
Risby Warren	170	ю	1 1	119*	114
Blaxton	150	9	341	209	202
Pompocali	1.7	т	136	112	115
Coniferized Pompocali Allerthorpe Common	2030	ю	212	167	2.3
Strensall	069	9	289	213	225
Crow	152	6	416	274	266
Charnwood Forest	11650	12	1 1	402**	402
Pre- coniferized Charnwood Allerthorpe Forest Common	2030	01	514	381	379
Sherwood	390	6	1 1	290*	ne 296 3.0
Sherwoo	Area (ha) No. species	No. national scarce and rare species	Regional scheme Quality score Sp. quality score	Ball's national scheme Quality score Sp. quality score	Archer's national scheme Quality score Sp. quality score

*Regional notable species based on Watsonian Yorkshire.

^{**}Regional notable species based on Archer (1990a).

For the eight Yorkshire localities the regional species quality score and Archer national species quality score from each locality show a significant linear positive relationship (correlation coefficient, r=0.84, p<0.01). Similarly, the regional quality score and Archer national quality score from each locality show a highly significant linear positive relationship (r=0.98, p<0.001). These relationships, in non-mathematical terms, indicate that the ranking—the order of the eight localities (best, 2nd, 3rd . . . 8th)—based on the regional scores are similar to the rank order based on the Archer national scores. At present these relationships cannot be explored outside Watsonian Yorkshire as regional statuses for other parts of England are not yet available.

The regional species quality score and regional quality score are higher for each locality than the Archer national species quality score and Archer national quality score (Table 8) because there are four, rather than three, statuses before the national scarce species (Tables 3 and 5).

The three most popular criteria for the evaluation of wildlife importance are diversity, rarity, and area (Usher, 1986). The current investigation measures diversity, rarity, and area (Usher, 1986). The current investigation measures diversity by species richness, or the number of species; rarity by the species quality scores, and the number of national scarce and rare species; and area by the area of each locality in hectares (Table 8). Quality scores combine diversity and rarity in one measurement.

There are some measurement problems in these criteria. It is difficult to know if the species list for a locality is complete. Rarity status is not a static parameter as the distributions and abundances of species change with time, sometimes in cycles. The area of a locality is not always easy to measure, particularly when its boundaries are not clear because the surrounding habitats are similar to those on the locality, e.g. as at Blaxton Common, and Risby Warren.

For each of the 11 locations in Table 8 the number of species shows a highly significant linear correlation with both the number of nationally scarce and rare species (r=0.94, p<0.001) and the Archer national quality scores (r=0.95, p<0.001). Thus, the larger the diversity the increased chance there is of finding nationally scarce and rare species. These relationships are probably a reflection of a species-area relationship when the number of species increases as area increases. A plot of number of species as a natural logarithm (ln) versus area in hectares as a natural logarithm (ln) gives a highly significant linear relationship (r=0.86, p<0.001). Removing the data for coniferized Allerthorpe Common, which is a damaged habitat (Archer, 1989), increases the significance of the species-area relationship (r=0.90, p<0.001), (Fig. 1) and gives the species-area regression equation. $\ln S = 3.87 + 0.11 \times \ln A$, where S = number of species and A = area in hectares. Thus the larger the area of the locality the more species are present.

The positive relationship between diversity and rarity on sandy heathland habitats is probably related to the thermophilic requirements of aculeate wasps and bees. Dry sandy habitats, particularly with sheltered banked open areas facing southwards, are able to warm up quickly in sunlight, and provide excellent nesting and foraging resources. With an increase in area of such sandy habitats, environmental heterogeneity will tend to increase so that more species will be able to find their specific resources which are more likely to persist from year to year. Disturbance of sandy habitats by rabbit burrowing, public pressure within limits or the digging of sand pits increases the habitat's suitability for aculeate wasps and bees.

Ball (1992) showed a negative relationship between diversity and rarity for lowland peat bog habitat. Peat bogs have low species richness but many of the species are restricted to peat bogs. Since peat bogs are a rare habitat the bog specialities are rare

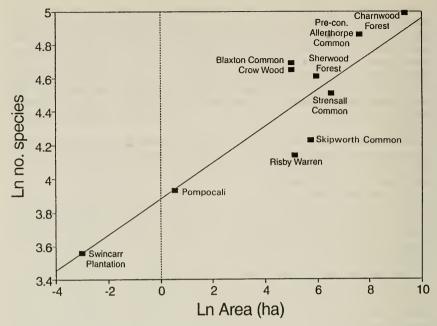


Fig. 1. The number of species as a natural logarithm (ln) versus area (ha) as a natural logarithm (ln) of the species of solitary wasps and bees recorded from sandy habitats in Watsonian Yorkshire and elsewhere in England. The regression line is given by $\ln S = 3.87 + 0.11 \times \ln A$, where S = number of species and A = area in hectares.

species. Disturbance of a peat bog by peat cutting or increasing drainage increases diversity, but the rare species tend to be lost.

Thus the relationship between diversity and rarity may be positive or negative. This observation has implications for the conservation of wildlife. The aim of increasing diversity within a particular habitat may or may not be suitable, depending on the type of habitat and group of organisms to be conserved.

CLEPTOPARASITIC LOAD

Wcislo (1987) showed that the amount of parasitic behaviour among aculeate Hymenoptera correlated with geographical latitude, being higher in the temperate compared with the tropical regions. If this is the case, since England and Wales occupy less than 6° of latitude then the CLs for localities in England and Wales should have similar values. Table 9 shows the CLs for the 11 data sets of sandy habitats. The CLs of the solitary wasps all have a similar value (range 13.2–20.0) as do the solitary bees (range 25.0–36.6). The higher CL for the solitary bees versus the solitary wasps is a function of the British fauna and is probably a consequence of food-chain relationships. Host solitary wasp species are the less numerous secondary consumers and thus less likely to support cleptoparasitic species, while the host solitary bee species are the more numerous primary consumers and thus more likely to support cleptoparasitic species.

Table 9. A comparison of the cleptoparasitic loads and nesting habits of the species of solitary wasps and bees of sandy habitats in Watsonian Yorkshire and elsewhere in England.

	Cleptoparasitic loads		Aerial nester frequency	
	Wasps	Bees	Wasps	Bees
Sherwood Forest	17.6	25.0	47.6	19.4
Pre-coniferized				
Allerthorpe Common	16.9	32.8	45.3	16.3
Charnwood Forest	18.1	27.0	71.2	22.2
Crow Wood	16.9	28.9	20.4	9.4
Strensall Common	18.0	35.0	41.5	19.2
Coniferized				
Allerthorpe Common	13.9	35.9	20.0	8.0
Pompocali	20.0	36.6	12.5	0.0
Blaxton Common	15.0	26.5	43.1	13.9
Risby Warren	17.2	29.4	12.5	8.3
Skipwith Common	13.2	35.5	42.4	30.0
Swincarr Plantation	16.7	34.8	0.0	6.7
British Isles	17.8	26.0	44.9	19.0

AERIAL NESTER FREQUENCY

The AFs of the species of solitary wasps (range 0.0–71.2) and solitary bees (0.0–30.0) from the 11 data sets are rather variable (Table 9). Much of the variation of AFs is dependent on the availability of aerial nesting sites (Archer, 1993b), but the higher solitary wasp aerial nester frequency of Charnwood Forest could be related to its higher altitude, where average temperatures and amounts of sunshine would be reduced. Under such weather conditions, aerial nesting sites are likely to warm up quicker and be warmer for a longer time than subterranean sites. Lomholdt (1975) showed that aerial nester frequency increased with increasing latitude for Sphecidae (28% in France and 79% in northern Norway) along a decreasing warmth gradient. It is unlikely that much of the variation of AFs is dependent on the availability of subterranean nesting sites because all localities under study are sandy habitats and personal investigation has shown that such habitats are very favourable to subterranean nesters.

The higher AFs for solitary wasps compared with solitary bees are a function of the British fauna and are probably a consequence of the cooler English climate. It is known that the activities of solitary wasps are more affected by weather conditions than those of solitary bees in England (Archer, 1990b) so that as explained by the altitude effect, solitary wasp species are more likely to be successful as aerial nesters.

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APPENDIX. ACULEATE WASP AND BEE SPECIES RECORDED FROM CROW WOOD

* Yorkshire rare species. ** Yorkshire local species.

Dryinidae. Aphelopus melaleucus (Dalman), A. serratus Richards, Anteon arcuatum (Kieffer), A. brachycerum (Dalman), A. ephippiger (Dalman), A. flavicorne (Dalman), A. fulviventre (Haliday), A. gaulei (Kieffer), A. jurineanum Lat., A. pubicorne (Dalman), A. tripartitum Kieffer, Lonchodryinus ruficornis (Dalman), Gonatopus sepsoides Westw., Pseudogonatopus distinctus (Kieffer).

Bethylidae. Bethylus cephalotes Förster, B. fuscicornis (Jurine).

Chrysididae. Omalus auratus (L.), Chrysis angustula Schenck, C. ruddii Shuck.**, C. impressa Schenk, Chrysis cyanea (L.), Hedychridium ardens (Lat.)**, Cleptes semiauratus (L.)*. Mutillidae. Myrmosa atra Panz.

Pompilidae. Priocnemis exaltata (F.), P. perturbator (Harris), P. parvula Dahlbom, P. schioedtei Haupt, Pompilus cinereus (F.)**, Arachnospila anceps (Wesm.), A. trivalis (Dahlbom), A. spissa (Schiødte), Anoplius concinnus (Dahlbom), A. viaticus (L.)**, A. infuscatus (V.d.Lind.)*, Evagetes crassicornis (Shuck.).

Eumenidae. Ancistrocerus parietinus (L.), A. oviventris (Wesm.), A. scoticus (Curt.), Symmorphus mutinensis (Baldini).

Vespidae. Dolichovespula sylvestris (Scop.), Vespula austriaca (Panz.), V. rufa (L.), Paravespula germanica (F.), P. vulgaris (L.).

Sphecidae. Astata pinguis (Dahlbom), Tachysphex pompiliformis (Panz.)**, T. unicolor (Panz.)*, Trypoxylon attenuatum Smith, F., T. figulus (L.), Crabro cribrarius (L.)**, C. peltarius (Schreb.)**, Crossocerus elongatulus (V.d.Lind.), C. ovalis Lepel. & Brullé, C. palmipes (L.)*,

C. tarsatus (Shuck.), C. varus Lepel. & Brullé, C. wesmaeli (V.d.Lind.), C. nigritus (Lepel & Brullé), C. quadrimaculatus (F.), Lindenius albilabris (F.), Entomognathus brevis (V.d.Lind.), Rhopalum coarctatum (Scop.), Oxybelus uniglumis (L.)**, Psen dahlbomi (Wesm.), P. bicolor Jurine*, P. equestris (F.)**, P. lutarius (F.)*, Pemphredon inornatus Say, Diodontus luperus Shuck.*, D. minutus (F.)**, D. tristis (V.d.Lind.)**, Passaloecus singularis Dahlbom, Ammophila sabulosa (L.)**, Mellinus arvensis (L.)**, Nysson spinosus (Forster), N. trimaculatus (Rossius)*, Gorytes quadrifasciatus (F.), G. tumidus (Panz.), Argogorytes mystaceus (L.), Cerceris arenaria (L.)*.

Colletidae. Colletes fodiens (Geoff.), Hylaeus communis Nylander, H. brevicornis Nylander*. Andrenidae. Andrena clarkella (Kirby)**, A. fulva (Müller), A. jacobi Perkins, A. bicolor F., A. angustior (Kirby), A. nigroaenea (Kirby), A. haemorrhoa (F.), A. tibialis (Kirby)*, A. barbilabris (Kirby)**, A. chrysosceles (Kirby), A. humilis Imhoff, A. minutula (Kirby), A. saundersella Perkins, A. subopaca Nylander, A. ovatula (Kirby)*, A. wilkella (Kirby), Panurgus

banksianus (Kirby)*.

Halictidae. Halictus rubicundus (Christ), H. tumulorum (L.), Lasioglossum leucozonium (Schr.), L. calceatum (Scop.), L. nitidiusculum (Kirby), L. punctatissimum (Schenck), L. rufitarse (Zett.), L. villosulum (Kirby), L. leucopum (Kirby), Sphecodes fasciatus von Hagens, S. gibbus (L.), S. monilicornis (Kirby), S. pellucidus Smith**.

Megachilidae. Osmia leaiana (Kirby), Megachile versicolor Smith.

Anthophoridae. Nomada fabriciana (L.), N. flavopicta (Kirby)*, N.fulvicornis (F.)*, N. goodeniana (Kirby), N. leucophthalma (Kirby)**, N. marshamella (Kirby), N. panzeri Lepel., N. striata F., Epeolus variegatus (L.), Anthophora furcata (Panz.).

Apidae. Bombus lucorum (L.), B. terrestris (L.), B. lapidarius (L.), B. pratorum (L.), B. hortorum (L.), B. pascuorum (Scop.), Psithyrus bohemicus (Seidl), P. vestalis (Geoff.), Apis mellifera L.

BOOK REVIEWS

The insects: an outline of entomology by P. J. Gullan and P. S. Cranston. Chapman & Hall, London, 1994, xiv + 491 pages, £24.99, paperback.—The history of entomology has been one of increasing fragmentation and specialization. General texts, like this one, serve primarily to inform students; but also they provide a means by which specialists can update themselves by access to a modern framework for insect science. The writers have succeeded in compiling a well-integrated book, attractively presented and very reasonably priced.

The volume is divided into 15 chapters. After an introduction on the importance and diversity of insects, which incorporates a table with brief characterizations of the 29 orders recognized, there follow seven chapters dealing, broadly speaking, with structure, function and development. External anatomy is reviewed briefly in chapter 2, followed (chapter 3) by a treatment of internal anatomy and related physiological function. Sensory systems and the main components of insect behaviour are described in chapter 4. Reproduction is the subject of a chapter (5) to itself and incorporates the relevant aspects of behaviour, morphology, physiology and the diversity of modes of reproduction (e.g., parthenogenesis, neoteny, polyembryony). It is followed, logically enough, by insect development and life histories (chapter 6), which considers not only the expected topics such as ontogeny, voltinism and polymorphism, but also examines how an understanding of certain environmental factors affecting development can be applied to model predictively insect abundance and distribution.

Chapter 7, on insect systematics, phylogeny and evolution, is followed by eight chapters, shifting the course of the book to somewhat broader entomological themes. The first two of these chapters (8 and 9) deal with aspects of insect biology in particular habitats—the soil (including also litter, carrion and dung) and water. Chapter 10 is